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RESEARCH ARTICLE

Causes and consequences of liana infestation in southern Amazonia

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Abstract

1. Lianas, a key component of tropical forests, can limit growth of trees, impacting both the structure and functioning of forests, and are expected to benefit from fragmentation and potentially from global climatic changes. While it is critical to understand the impacts of liana infestation on contemporary tropical forests across large geographical areas, to date most liana studies have been focussed on single or few sites.
2. We measured and quantified liana infestation of 16,066 trees with diameter ≥10 cm in 27 plots distributed across southern Amazonia, a region characterized by substantial ecological and environmental variation and environmental change. We examined the influence of potential drivers of liana infestation at the plot, species and individual tree level. Additionally, we evaluated the effect of liana infestation on tree growth.
3. More than half of all trees had lianas in their crown. At the plot level, infestation by lianas was driven by forest structure but not by the studied climate or soil fertility variables, though low levels of liana infestation were found in seasonally flooded forests.
4. At the tree level, larger and stouter trees had a greater proportion of their crown infested with lianas. At the species level, trees belonging to intrinsically slow-growing, dense-wooded species were more susceptible to liana infestation.
5. Liana infestation had a negative impact on tree growth, with growth of heavily infested trees reduced by 33% compared to non-infested. The impact of liana infestation on tree growth was strongest for the best-lit tree crowns, indicating that

lianas act to reduce the large competitive advantage that well-lit trees otherwise hold over their neighbours.

6. *Synthesis*. Lianas are a pervasive and influential feature of the extensive forests at the southern edge of Amazonia. The degree of liana infestation in forests was closely linked to species-level variables such as potential growth and wood density as well as the size of the individual tree. The growth of heavily infested trees was particularly restricted by lianas, and especially so for trees growing in otherwise favourable conditions, indicating the potential for lianas not only to reduce forest growth rates overall, but also to modify competitive hierarchies among trees within tropical forests.

KEYWORDS

biomass, climate change, forest structure, habitat fragmentation, soil, tree mortality, wood density

1 | INTRODUCTION

Lianas are not only a major floristic component of tropical forests, but by using trees for support they also play a significant role in determining tropical forest structure, dynamics and ecosystem function. For example, once they reach the tree crowns, lianas can create dense foliage that reduces the light available for the trees below (Clark & Clark, 1990; Fauset et al., 2017), which consequently affects tree carbon sequestration and growth (Clark & Clark, 1990; Schnitzer & Carson, 2010; Visser et al., 2018) and reduces total forest biomass (Phillips et al., 2002; Tymen et al., 2016). Lianas can directly damage host trees, for example by breaking branches and stems, which in turn creates canopy gaps which increases light availability on the forest floor that favours the establishment of lianas (Laurance et al., 2014; Phillips, Martínez, Mendoza, Baker, & Vargas, 2005; Schnitzer, Dalling, & Carson, 2000). Lianas also strongly compete below-ground with trees, particularly with fast-growing species that require more water and soil nutrients than slow-growing species (Campanello et al., 2016; Visser et al., 2018).

Potential host trees vary in their susceptibility to lianas. For example, the degree of liana infestation may increase with the size of the host trees (Fadrique & Homeier, 2016; Sfair, Ribeiro, Pimenta, Gonçalves, & Ramos, 2013), and some species tend to be more infested by lianas than others (van der Heijden, Healey, & Phillips, 2008). Shade-tolerant species may be at particular risk of liana infestation due to their slow growth (Laurance et al., 2001; van der Heijden et al., 2008). Characteristics of the forest itself may therefore be more important than the physical environment in controlling the success of lianas in tropical forests (Poulsen et al., 2017; van der Heijden & Phillips, 2008). However, no attempt has yet been made to evaluate the importance of soil fertility, climate, fragmentation and host characteristics in determining the degree of liana infestation in tropical forests in a single analysis.

Across many tropical forests an increase in the abundance and biomass of lianas has been observed over recent decades (Laurance et al., 2014; Phillips et al., 2002; Schnitzer & Bongers, 2011). Changing climatic conditions that include lengthening of dry seasons (e.g. DeWalt et al., 2010; van der Heijden, Powers, & Schnitzer, 2019) provide one leading potential explanation for this. As lianas can exert strong stomatal control by which carbon fixation is maximized whilst minimizing water loss (Cai, Schnitzer, & Bongers, 2009; Campanello et al., 2016), they are hypothesized to derive a growth advantage over trees particularly in forested tropical areas with high climatic seasonality and relatively low rainfall (DeWalt et al., 2010; Schnitzer, 2005; Schnitzer & Bongers, 2011; Schnitzer & van der Heijden, 2019). Other potential explanations for the increase in liana infestation include increasing wind disturbance, which could drive large-scale shifts in liana-tree ecology, favouring predominantly fast-growing, light-demanding life-forms such as lianas (e.g. Laurance et al., 2014; Phillips & Gentry, 1994; Schnitzer & Bongers, 2011) and direct effects of elevated CO_2 conditions that increase the vigour of lianas over those of trees (Granados & Korner, 2002). Direct and indirect effects of elevated atmospheric CO_2 concentrations may therefore favour liana growth and shorten the life cycle of trees, affecting mortality rates and accelerating forest dynamics (e.g. Brienen et al., 2015; Granados & Korner, 2002).

The increasing disturbance of tropical forests due to selective logging, fire and fragmentation may also drive liana proliferation (e.g. Campbell et al., 2018; Laurance et al., 2001). Following fragmentation, trees at forest edges are exposed to greater wind speeds, higher temperatures and reduced humidity, which can damage trees and open the forest canopy. After fragmentation, deposition of nutrients related to the burning of biomass and adjacent application of agricultural fertilizers increases the soil fertility and may favour the establishment of lianas, particularly in edges and smaller fragments (Laurance et al., 2001; Magnago et al., 2017; Moreira, Nóbrega, Conceição Jesus, Ferreira, & Pérez, 2009). Most species of lianas

have flexible stems, which may increase their success in fragmented forests (Putz, 1984a).

The combination of climate change and fragmentation is likely to be manifested differently in different parts of the tropics. Thus far, however, detailed studies of liana demography and impacts are few and have concentrated on one or a few intensively studied sites (e.g. Ingwell, Joseph Wright, Becklund, Hubbell, & Schnitzer, 2010; Laurance et al., 2014; Phillips et al., 2005; Tymen et al., 2016). In southern Amazonia, fragmentation and climate change are affecting forests (Alencar, Brando, Asner, & Putz, 2015; Nogueira, Fearnside, Nelson, Barbosa, & Keizer, 2008; Reis et al., 2018) that are often already naturally 'hyperdynamic', with higher baseline mortality and recruitment rates when compared to most of Amazonia (Marimon et al., 2014). The highly dynamic natural environment, seasonal climate and propensity to drought (Feldpausch et al., 2016; Fu et al., 2013; Gloor et al., 2015; Jiménez-Muñoz, Sobrino, Mattar, & Malhi, 2013; Marengo, Tomasella, Alves, Soares, & Rodrigues, 2011) of the southern Amazon may together mean that this region is more prone to liana infestation than other regions. The rapid changes in the region further provide us with a unique opportunity to better understand how lianas interact with other drivers of forest ecology and change.

Here we evaluated for the first time which factors explain the degree of liana infestation and the effects of lianas on tree growth at the southern border of Amazonia. We used multiple permanent plots monitored over time and distributed over much of the region to explore the potential causes of liana infestation and investigate a wide range of potential drivers, related to tree size, tree form (height to diameter ratio) and identity, as well as forest-level resource and fragmentation attributes. Additionally, we assessed the consequences of infestation by investigating tree-level growth trajectories and their potential drivers. We used this information to contribute to tackling two fundamental questions to understand the ecology and impacts of lianas in tropical forests: (a) *What factors determine liana infestation in tropical trees, species and forests?* (b) *How important are the impacts of lianas on tree growth relative to other well-known determinants, such as tree size, wood density and light environment?* Based on studies cited above we anticipated that liana infestation will be: (a) positively related to key forest structural variables (tree diameter, height, basal area, density, percentage of broken trees); (b) negatively associated with growth rate of tree species, and consequently (c) positively related to wood density of tree species; (d) negatively related to precipitation and (e) positively related to maximum climatological water deficit, (f) positively related to soil fertility and (g) to fragmentation (e.g. fragment area, edge distance) and (h) negatively related to tree-level growth rate.

2 | MATERIALS AND METHODS

2.1 | Study area

We studied 27 forest inventory plots distributed over approximately 25,000 km^2 of land across the southern border of Amazonia (Figure 1; Table S1). The climate in this region corresponds to the *Aw* (tropical with dry winters) and *Am* (tropical monsoon) types in the Köppen's classification system (Alvares et al., 2013). Mean annual precipitation and the mean monthly temperature ranged from ~1,500 to 2,400 mm and ~24.1 to 27.3°C respectively (spatial resolution of 1,000 m; *WorldClim* 1.4; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005; Table S1). Elevation ranged from 177 to 400 m a.s.l. (Table S1).

2.2 | Data collection and preparation

In each forest, we demarcated an inventory plot of one hectare. Plots were regionally distributed to cover major geographical gradients and were established between 2008 and 2016 within protected areas in private and public land. Eight plots were in forests that are seasonally flooded and occasionally affected by fire. The other 19 plots had no recent record of fire and three of them were seasonal evergreen forest on anthropogenic black earth, which originated from anthropic addition of organic matter (OM) or household wastes, ceramic artefacts and charcoal to the soil by pre-Columbian civilization (Sombroek et al., 2002). For each plot, all trees were recensused every 2–4 years and liana infestation data were collected between 2010 and early 2016 (Table S1).

We identified and tagged all woody stems with a diameter at breast height (*D*) ≥10 cm, that is, at 1.3 m height or above any stem deformity, in each plot. We encountered a total of 16,066 trees. We measured the diameter, total height and the liana crown occupancy index (COI) of each tree following the standard protocols of the RAINFOR network (Peacock, Baker, Lewis, Lopez-Gonzalez, & Phillips, 2007; Phillips, Baker, Feldpausch, & Brienen, 2018). The liana COI was estimated visually and classed into five categories, where 0 = no lianas in the crown, 1 = 1%–25% of the crown covered by lianas leaves, 2 = 26%–50% of the crown covered, 3 = 51%–75% of the crown covered and 4 > 75% of the crown covered. This semi-quantitative liana crown occupancy index has been shown to accurately measure individual tree and plot-level liana loads elsewhere (van der Heijden, Feldpausch, de la Fuente Herrero, van der Velden, & Phillips, 2010). We also estimated the crown illumination index (CII) visually, where: 2a = low and 2b = medium and 2c = high lateral light—*Low light*; 3a = some vertical light (<50%), 3b = high vertical light (>50%)—*Medium light*; 4 = crown completely exposed to vertical light, 5 = crown completely exposed to vertical and lateral light—*High light* (adapted from Clark & Clark, 1992). All tree and liana data are deposited in the ForestPlots.net database (Lopez-Gonzalez, Lewis, Burkitt, & Phillips, 2011).

We collected samples of botanical material for each tree species for identification. We identified tree species through comparing the voucher material with that available in herbaria, and through consultations with specialists. Botanical family nomenclature was based on APG-Angiosperm Phylogeny Group (2009). We deposited the botanical specimens in the permanent collections of the Herbarium NX (UNEMAT—Nova Xavantina campus, Mato Grosso). Species

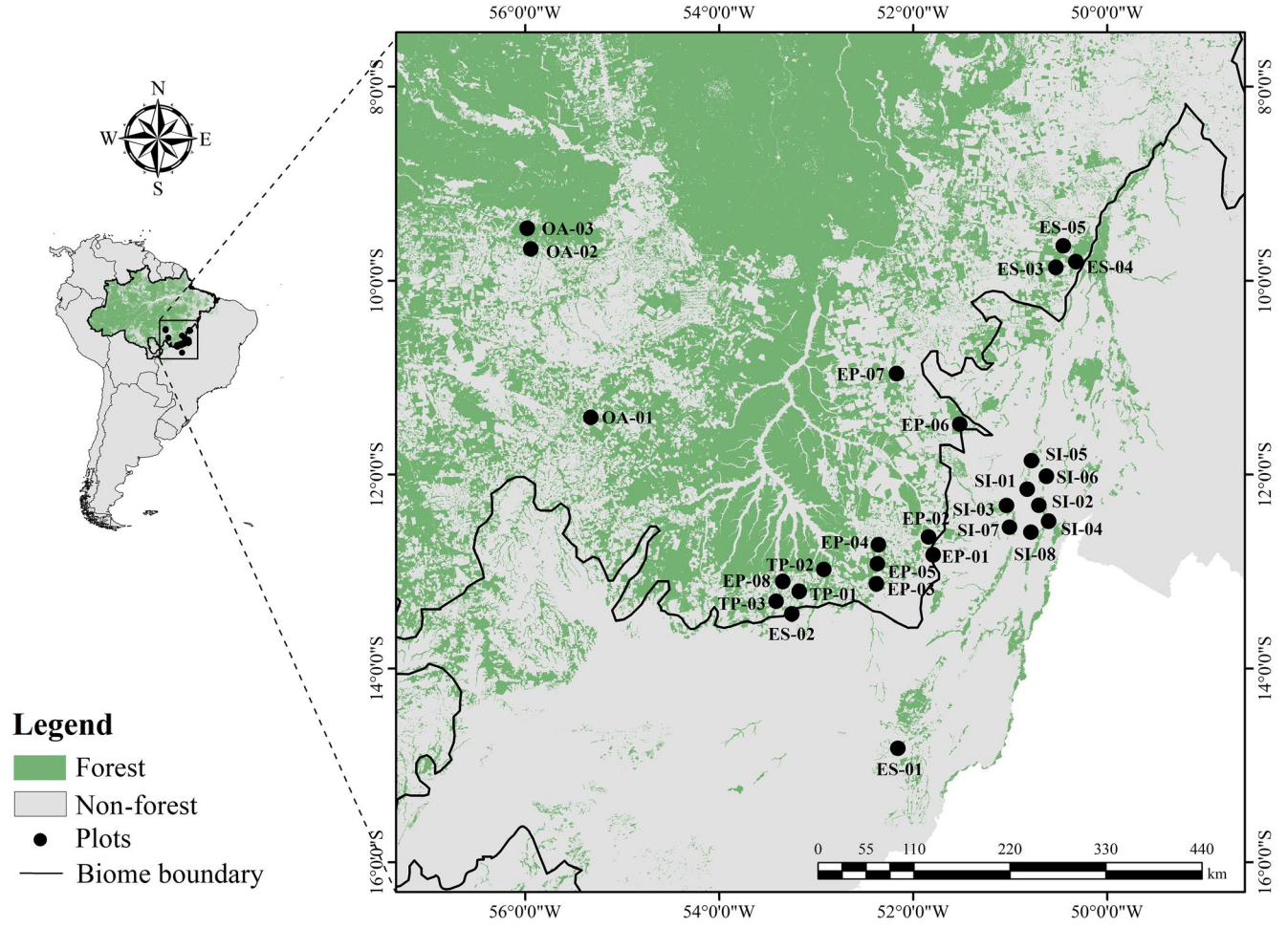

FIGURE 1 Location of the plots sampled in the southern Amazon border, between eastern and northern Mato Grosso and southern Pará, Brazil, showing the approximate biome (Cerrado and Amazonia) boundaries (black line) based in IBGE-Instituto Brasileiro de Geografia e Estatística (2004). The classification of forest and non-forest was based on the PRODES project (INPE-Instituto Nacional de Pesquisas Espaciais, 2017). All sampled plots lie within mature, evergreen or semi-deciduous forest fragments. For display purpose we had slightly separated points where plots are overlapping. EP, *floresta estacional perenifólia* (seasonal evergreen forest); TP, *floresta estacional perenifólia em terra preta de Índio* (seasonal evergreen forest on anthropogenic black earth); ES, *floresta estacional semidecidual* (seasonal semi-deciduous forest); OA, *floresta ombrófila aberta* (open rainforest); SI, *floresta sazonalmente inundável* (seasonally flooded forest) [Colour figure can be viewed at wileyonlinelibrary.com]

names were revised using the Brazilian List of Plant Species (2016; http://floradobrasil.jbrj.gov.br) and data on wood density for each species was obtained from a world database (Chave et al., 2009; Zanne et al., 2009). When species-level wood density was not available we used the appropriate average genus-level wood density, and for those identified only to genus (10.9% of species) or family (0.5% of species) we used the average wood density of these taxonomic groups (Flores & Coomes, 2011; see also Supporting Information). We used the average trait value of the community for the small proportion of individuals (0.8%) belonging to families for which no wood density information was available.

To evaluate potential effects of precipitation on liana infestation (percentage of trees infested by lianas), we obtained data (Table S2) from the *WorldClim* 1.4 database, with a spatial resolution of 1,000 m, based on the data collected by meteorological stations between 1950 and 2000 (Hijmans et al., 2005). We used data from the Tropical Rainfall Monitoring Mission (TRMM; NASA, 2012) to derive the mean value of the maximum climatological water deficit (MCWD; see equation in Aragão et al., 2007) between 1999 and 2011, also including the droughts of 2005, 2007 and 2010. The MCWD index is calculated from cumulating monthly water deficits, which represent the difference between monthly precipitation and evapotranspiration. We used a fixed monthly ET value of 100 mm to calculate each monthly deficit, a metric of dry season intensity (cf. Aragão et al., 2007).

To evaluate the effect of habitat fragmentation and distance to nearest fragment edge on the percentage of liana infested trees, we measured the size of each fragment in which plots were located and the distance from each plot to the nearest fragment edge. The plots were located between 1 and 5,440 m from the nearest edge of the forest fragment, and the fragments themselves varied in size from 5 to 45,459 ha (Table S1; Reis et al., 2018 for details).

We also evaluated the potential effects of soil fertility on the percentage of infested trees. To do this we collected, in each plot,

five soil samples from the surface layer (0–10 cm). The samples were dried at ambient temperature for 3–4 days and analysed regarding their chemical components (pH, OM, concentration of Al, P, K, Ca and Mg; see Table S2 for details). Chemical analyses followed standard protocols (EMBRAPA-Empresa Brasileira de Pesquisa Agropecuária, 1999). Following this procedure, we calculated the average of each chemical parameter per plot. For two plots (FOA-02 and 03, see Table S2), we used soil data from ForestPlots.net database (https://www.ForestPlots.net/), which follows a similar methodology. For the seasonally flooded forest-plots, 20 soil samples were collected, 10 being from subplots adjacent to border and 10 from subplots close to the fragment centre. For soil fertility, we used OM—plant and animal detritus in various phases of decomposition—and base saturation (BS), which is the percentage of cation exchange capacity of basic cations (Ca, Mg, K, Na) in soil and provides a good index of soil fertility (e.g. Poulsen et al., 2017).

Lianas often damage trees, breaking the tree branches and stems (e.g. Putz, 1984a). We tested the association between the percentage of infested trees and the percentage of broken trees among plots, in the last census, by calculating the percentage of the trees with broken trunks and/or those with more than 75% of the crown broken off. To evaluate the potential effects of forest structure variables on the percentage of infested trees at plot level, we calculated the diameter, height and slenderness (*H*:*D* ratio) as the 95th percentile of all tree individuals (e.g. Fauset et al., 2015).

We used all 13 terra firme plots for which we had tree data available for at least two censuses to describe the effect of tree species properties, such as wood density and growth, on liana infestation. Since lianas are known to reduce tree growth rate (e.g. Clark & Clark, 1990), using species-specific growth rate averages based on trees both with and without lianas may confound results (van der Heijden et al., 2008). Thus, we computed the potential growth rate of each tree species with ≥20 individuals which had at least five liana-free individuals (51 species) across the region, as our measure of species-specific growth rate. We calculated the potential growth rate for each species (cm/year) as the 95th percentile of the five or more liana-free trees between the latest two censuses (e.g. Fauset et al., 2015; van der Heijden et al., 2008).

To evaluate the effect of the liana crown occupancy index on tree growth rate, we used the same 13 plots described above. We calculated tree diameter growth rate (cm/year) by dividing the difference in diameter between the first and the second census by the time interval (in years). We used the two most recent censuses, because we wanted to control for the potential effects of time-related trends in tree growth and liana infestation previously reported in Amazonia (e.g. Brienen et al., 2015; Phillips et al., 2002) and impacts of large-scale inter-annual climate anomalies on annual growth (e.g. Doughty et al., 2015; Phillips et al., 2009; Rowland et al., 2014).

2.3 | Data analysis

We investigated the drivers of liana infestation at the scale of the tree community (plot level), species (taxon level) and for individual trees (tree level). Additionally, we also investigated the influence of liana infestation on tree growth for different levels of crown illumination (tree level).

2.4 | Plot-level drivers of liana infestation

To access the influence of resources (e.g. precipitation and soil fertility), fragmentation (e.g. fragment area) and forest structure (e.g. tree density, percentage of broken trees; Table 1) on liana infestation (percentage of trees infested by lianas; response variable) at the plot level, we used GLM (family = *quasipoisson*) using LME4 package (Bates, Maechler, Bolker, & Walker, 2015). We fitted all subsets of the general linear model with explanatory variables and then averaged the subset of models where $\Delta AIC < 4$. We performed multimodel inference using the MuMIn R package (Barton, 2019). Prior to this analysis and the ones below (preliminary model Equations 1–3), we standardized the data and removed possible collinearity among predictors using Variance Inflation Factors (VIFs > 3; Quinn & Keough, 2002) and pairwise correlations. Because of collinearity, we had to exclude diameter, height, MCWD, BS, OM, edge distance and TB. After removing these variables all pairwise correlations were weak enough not to cause problems through collinearity ($r < 0.7$ and VIF < 3). Our preliminary model which we investigated was:

$$\begin{aligned}\text{Percentage of trees infested by lianas} \sim\ & \text{diameter (95th percentile)} \\ & + \text{height (95th percentile)} + \text{slenderness (95th percentile)} \\ & + \text{basal area (total)} + \text{tree density} + \text{precipitation} + \text{MCWD} + \text{BS} \\ & + \text{OM} + \text{species richness} + \text{fragment area} + \text{edge distance} + \text{TB}. \quad (1)\end{aligned}$$

Assumptions of normality and linearity for models were verified using graphical visualization of the residuals. We further assessed the spatial autocorrelation in the residuals for each model using Moran's *I* (Figure S3). No spatial dependence was detected among plots, which allowed us to consider the plots as independent samples in our analyses.

2.5 | Tree-level drivers of liana infestation

To access the most important factors (e.g. individual basal area, height, CII) in determining liana presence at the tree level (see Table 1), we developed general linear mixed effect models (Equation 2; GLME, family = *binomial*). We included diameter, height, slenderness, basal area and CII as fixed effects. To evaluate the height and slenderness relationship independently of damage, we excluded from our main analyses all trees with broken trunks or those with more than 75% of the crown broken off. Because of collinearity, we had to exclude height and basal area and after removing these variables the collinearity between the remaining variables was weak ($r < 0.7$ and VIF < 3). To account for the non-independence among genera as a consequence of their shared phylogenetic history, we included

TABLE 1 Potential drivers of liana infestation and tree growth at tree and plot level across the southern border of Amazonia. For soil variables: BS, base saturation; OM, organic matter (%). These variables were included as either fixed (*f*) or random (*r*) effects in the models. *95th percentile and **total basal area of the plot

Infestation driver	Variable candidate	Variable description	Plot level	Tree level	Growth drivers
Forest structure	*D*	Diameter at breast height (cm)	*f**	*f*	*f*
	H	Height (m)	*f**	*f*	*f*
	H:*D*	*H*:*D* ratio (slenderness)	*f**	*f*	—
	BA	Basal area (m^2)	*f***	*f*	—
	TD	Tree density	*f*	—	—
	TB	Trees with crown and/or trunk broken (%)	*f*	—	—
Resources	CII	Crown illumination index	—	*f*	*f*
	Prec	Precipitation (mm)	*f*	—	—
	MCWD	Maximum climatological water deficit (mm)	*f*	—	—
	Soil	Soil fertility—(BS and OM)	*f*	—	—
Identity	Family	Family	—	*r*	*r*
	Genus	Genus	—	*r*	*r*
	Species	Species	—	*r*	*r*
	SR	Species richness	*f*	—	—
	WD	Wood density (g/cm^3)	—	—	*f*
Fragmentation	FA	Fragment area (ha)	*f*	—	—
	ED	Edge distance (m)	*f*	—	—
Plot	Plot		—	*r*	*r*
Lianas		Liana crown occupancy index (COI)	—	—	*f*

phylogeny as a random effect as a nested design of family (*f*), genera within families (*gf*) and species within genera within families (*sgf*). As individual trees are clustered within plots, we also included the intercept of plot as random effects:

$$\text{Liana (presence and absence)} \sim \text{diameter} + \text{height} + \text{slenderness} + \text{basal area} + \text{CII} + (1|\text{family/genus/species}) + (1|\text{plot}). \quad (2)$$

In the analysis described above, we observed that diameter, slenderness and light were important predictors of liana infestation at the individual tree level. Thus, we performed a complementary analysis to test whether these three variables also impacted the degree of infestation at the individual species level. For this complementary analysis, we used each tree species with a total of at least 40 individuals across our plots.

2.6 | Taxon-level drivers of liana infestation

We investigated whether intrinsic species growth potential can explain the degree to which species was affected by lianas by testing for the association between the percentage of individuals infested by lianas and their potential diameter growth rate (cm/year) and wood density (g/cm^3) using a linear regression. We used the same analysis to test the association between susceptibility to liana infestation of species (higher proportion of trees infested by lianas) and the degree of liana infestation (>0% of the crown).

2.7 | The effect of lianas on tree growth rate

We modelled tree growth and estimated the importance of lianas as a predictive variable when compared to variables known to influence tree growth (see Table 1). Our model was developed using a LME framework, including initial tree diameter (D_{t0}) and height (H_{t0}), wood density, CII and COI as fixed effects. As for the Equation 2, phylogeny was included in both models as a random effect—a nested design of *f*, *gf* and *sgf*—and plot as well as:

$$\text{Growth rate} \sim D_{t0} + H_{t0} + WD + \text{CII} + \text{COI} + (1|\text{family/genus/species}) + (1|\text{plot}). \quad (3)$$

The effect of liana infestation on tree diameter growth may be slightly reduced for trees with lighter wood and amplified for trees with higher wood densities (van der Heijden & Phillips, 2009). Thus, in our final model we included only those species that had wood density between 0.50 and 0.69 (g/cm^3) in order to control for potentially confounding factors of the fast–slow trait spectrum, and because this group of trees represents the largest sample size available, hence providing the greatest statistical power for distinguishing impacts

of canopy light and liana infestation. As tree diameter and height were strongly correlated ($R = 0.70$; $p < 0.001$), we excluded height from the final model to avoid collinearity. We conducted all analyses using R 3.6.0 (R Core Team, 2019). The main applied R packages were STATS, GOF (Holst, 2020), CAR (John Fox & Weisberg, 2011), LME4 (Bates et al., 2015) and GGPLOT2 (Wickham, 2016). We adopted a 5% significance level for all analyses.

3 | RESULTS

3.1 | Plot-level drivers of liana infestation

Overall, more than 50% of the 16,066 trees studied were infested by lianas across all 27 plots. Seasonally flooded forest (SI) plots were outliers in being least affected by lianas, while seasonal evergreen forest on anthropogenic black earth (TP) had the greatest infestation rates, but these (TP) were statistically no different from the other terra firme forests (Figure 2). In this paper, we concentrate on the terra firme results, excluding seasonally flooded forest plots from the analyses below, while also discussing flooded forests to illustrate their different behaviour.

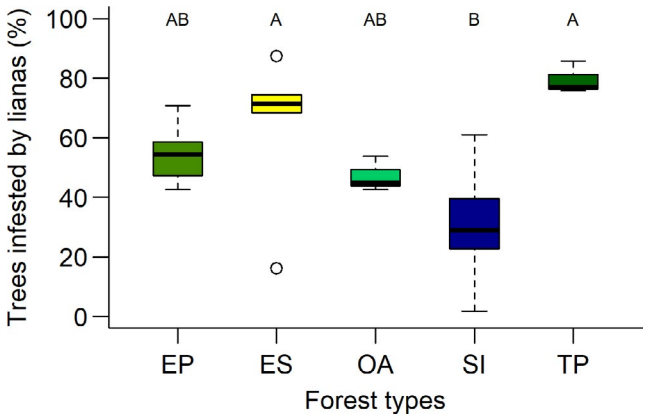

FIGURE 2 Percentage of trees infested by lianas in different forest types across southern Amazonia. Box-plots show plot-level values in each forest type, statistical comparisons are made among forest type analyses based on the ANOVA test ($F_{(4,22)} = 3.44$; $p = 0.02$). Different letters denote significantly differences by Tukey post hoc test. EP, seasonal evergreen forest; ES, seasonal semi-deciduous forest; OA, open rainforest; SI, seasonally flooded forest; TP, seasonal evergreen forest on anthropogenic black earth [Colour figure can be viewed at wileyonlinelibrary.com]

At the plot level, the percentage of trees infested by lianas was strongly related to forest structure (95th percentile slenderness of trees), but not to precipitation, soil fertility or fragmentation or other structural variables including basal area and number of stems (Figure 3; Table S4). The percentage of trees infested by lianas was higher in forests that had shorter trees for a given diameter—that is, trees that were less slender (Figure 3b).

3.2 | Tree-level drivers of liana infestation

At the tree level, liana infestation was most strongly related to slenderness and diameter of trees and light in the crown (Figure 4a). Highly infested trees had low height:diameter ratios and larger diameters (Figure 4b,c). The model with slenderness, diameter and light together was better (AICc = 10,371) than the model with diameter (AICc = 10,632), slenderness (AICc = 10,417) or light (AICc = 10,681) alone (Table S5), suggesting these variables had additional influences on liana infestation.

When we examined tree species at the population level across the region, we found that six of the seven most abundant species were significantly less slender when they were heavily infested (Figure S6). Notably, tree height per se did not vary consistently with liana crown occupancy (Figure S6). The tree individuals with larger diameters were less slender and had more light-exposed crowns (Figures S7 and S8).

3.3 | Taxon-level drivers of liana infestation

Liana infestation was negatively associated with the potential growth rate of tree species and positively associated with their wood density (Figure 5). Tree species with greater potential growth rate had less dense wood (Figure S9, $R = 0.48$, $p < 0.01$).

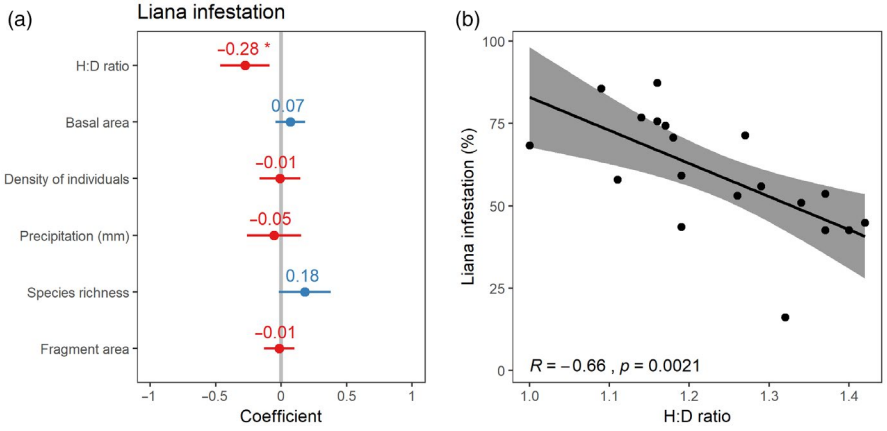

FIGURE 3 (a) Correlates of liana infestation (%) at the plot level across southern Amazonia. Points show coefficients from model-averaged GLM. Error bars show standard errors (thick lines). *$p < 0.05$. Coefficients are shown in Table S4. (b) Relationship between liana infestation (%) and slenderness, the only significant variable in the GLM model [Colour figure can be viewed at wileyonlinelibrary.com]

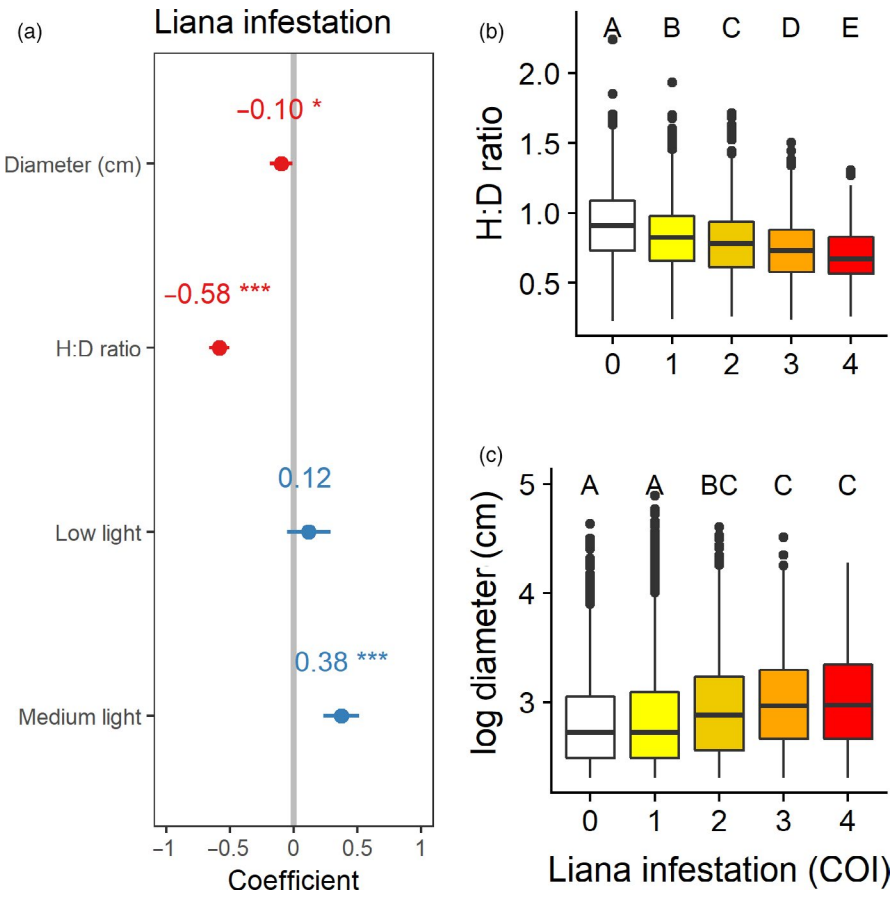

FIGURE 4 (a) Correlates of liana infestation (%) at the tree level across southern Amazonia. Points show coefficients from model-averaged GLM. Error bars show standard errors (thick lines). *$p < 0.05$. Coefficients are shown in Table S5. (b and c) Box-plots showing individual tree *H:D* ratio and diameter for each of liana infestation categories (canopy occupation index). Different letters denote significantly differences by Dunnett post hoc test [Colour figure can be viewed at wileyonlinelibrary.com]

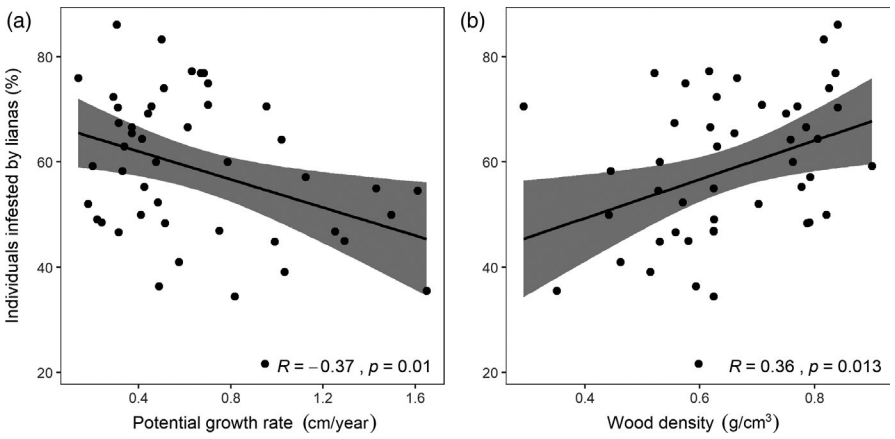

FIGURE 5 Relationship between tree species-specific liana infestation rates and potential growth rate (a) and wood density of these species (b). Analyses were restricted to those tree species with ≥20 individuals (51 species) which each had at least five non-infested trees sampled. Potential growth rate was calculated as the 95th percentile of growth rate of five or more non-infested trees and is therefore independent of liana infestation itself

Among the most dominant tree species, *Micropholis venulosa* (Sapotaceae) showed the highest susceptibility to liana infestation (78.3% of individual trees), followed by *Hymenaea courbaril* (Fabaceae; 70.4%) and *Hirtella glandulosa* (Chrysobalanaceae; 70.0%) while the fast-growing, light-wooded *Schefflera morototoni* (Araliaceae; 32.1%) and *Jacaranda copaia* (Bignoniaceae; 34.5%) were the least infested by lianas (Table S10). Those species more susceptible to liana infestation (i.e. with a greater proportion of trees infested by lianas) were also more often heavily infested (>50% of the crown occupied). The one exception was *Virola sebifera* (Myristicaceae), which was less susceptible to lianas in general (38.5%) with nearly half of these cases being heavily infested trees (Table S10; Figure S11).

3.4 | The effect of lianas on tree growth rate

Crown illumination, diameter and liana crown occupancy—but not wood density—were important predictors of diameter growth rate (Figure 6; Table S12). Tree growth was 33% slower for trees suffering heavy liana infestation (>75% of the canopy occupied) compared to trees without lianas (see Figure S13). Notably,

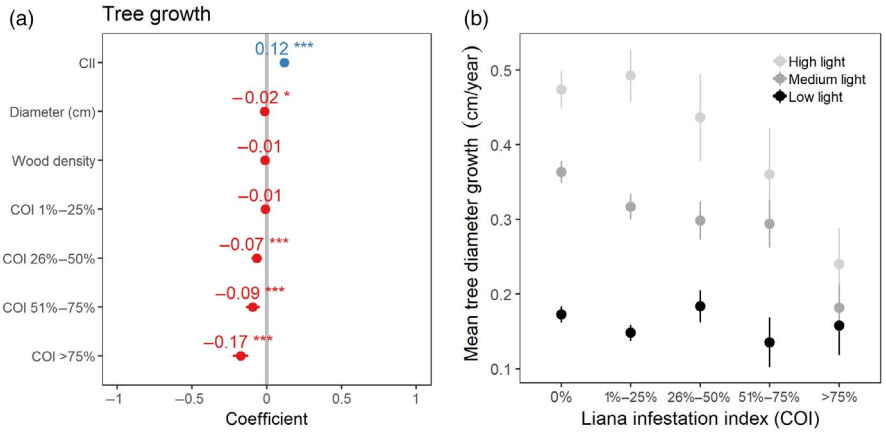

FIGURE 6 (a) Correlates of tree diameter growth rate (cm/year) in forests across southern Amazonia. Points show coefficients from model-averaged GLM. Error bars show standard errors (thick lines). $^{*}p < 0.05$ and $^{***}p < 0.001$. Coefficients are shown in Table S12. (b) Effect of liana crown occupancy index (COI) on tree diameter growth rate for different levels of crown illumination. Analyses were restricted to 2,320 trees with wood densities between 0.50 and 0.69 growing under different (CII; see Figure S13 for analysis including all trees). Dark, medium and light grey circles represent the average observed tree diameter growth rates under low, medium and full light respectively. Error bars represent ± 1 *SE* [Colour figure can be viewed at wileyonlinelibrary.com]

trees growing in high light conditions experienced more negative impacts of liana infestation than those with poorly lit canopies (Figure 6). Tree diameter growth rate was correlated with COI under medium ($\tau = -0.08$, $p < 0.05$) and full light ($\tau = -0.15$, $p < 0.05$), but not under low light ($\tau = -0.02$, $p > 0.05$). Similarly, highly infested trees always grew slowly regardless of the amount of light available (Figure 6).

4 | DISCUSSION

In forests across the southern border region of Amazonia, more than half of the 16,066 trees examined were infested by lianas, yet variation in plot-level infestation rates was not obviously influenced by environmental variables such as fragmentation, precipitation and soil fertility. Rather, the physical structure of the forest environment was important, with liana infestation greatest in forests that had trees with a high diameter to height ratio (95th percentile slenderness of trees). At the tree level, trees with such non-slender forms and larger in diameter were highly infested (>75% of the crown infested). At the species level, trees belonging to intrinsically slow-growing and dense-wooded tree species had an increased risk of becoming infested with lianas. Liana infestation in turn had a negative influence on tree growth, with trees growing in high light conditions experiencing more negative impacts of liana infestation having their growth especially strongly reduced.

4.1 | Drivers of liana infestation

4.1.1 | Flooding

This is the first study we are aware of the degree of liana infestation in any flooded tropical forest. These are important ecosystems, representing up to 4% of the Amazon Basin and so covering a total of 250,000 km^2 in Amazonia (Braga, 1979; Melack & Hess, 2010; WWF-World Wildlife Fund, 2019). We found that seasonally flooded forests have much lower liana infestation than other forests in southern Amazonia. The soils of our flooded forests had high aluminium concentrations, were acidic and had lower cation exchange capacity than other forests. Why were our flooded forests so little infested? Elsewhere in non-flooded Amazonia, reduced abundance and biomass of lianas was observed at one location to be associated with more acidic soils (Laurance et al., 2001), but other studies in Neotropical non-flooded forests have not detected an association between liana abundance and biomass and soil factors (Dalling et al., 2012; van der Heijden & Phillips, 2008). Alternatively, the low rate of liana infestation in seasonally flooded forests may be explained by the effect of seasonal flooding itself, which may limit lianas in their critical establishment phase (de Oliveira et al., 2014; van der Heijden et al., 2008). While we could not decouple the putative effects of soil chemical characteristics and seasonal flooding on liana infestation with our data, we can make clear predictions about the yet-to-be-assessed flooded tropical forests elsewhere. If soil cation concentrations are the critical factors, then we expect high levels of liana infestation in the high nutrient content flooded forests of western Amazonia (influenced by Andean uplift and weathering, in contrast to our ancient and tectonically inactive Brazilian Shield region). But if flooding provides the overriding physical limit on liana growth, then we expect low levels of liana infestation across tropical flooded ecosystems in general.

4.1.2 | Anthropogenic black earth

Evergreen forest on anthropogenic black earth (terra preta) had the very highest rate of liana infestation. An association between terra preta and liana infestation was observed before in the Amazon Basin

(Balee & Campbell, 1990). These soils were formed as a result of human occupation, being fertilized by discarded waste (Schmidt & Heckenberger, 2009) and having more organic carbon and higher levels of phosphorus, calcium and micronutrients than adjacent soils (Lehmann et al., 2003). To the extent that the higher concentration of phosphorus and OM in these sites may be supporting their high liana infestation rates, this suggests that, as with aspects of present-day tree species composition (Levis et al., 2017), ancient forest disturbance and management by pre-Columbian societies still influences liana infestation today (Balee & Campbell, 1990, see also Tymen et al., 2016).

4.1.3 | Precipitation and fragmentation

No effect of precipitation or habitat fragmentation on the percentage of trees infested by lianas was observed in our plots. While a negative association between liana abundance and precipitation had been observed across the tropics (DeWalt et al., 2010; Schnitzer, 2005), across 65 plots in the Neotropics liana, basal area and density were unrelated to annual precipitation or dry season length (van der Heijden & Phillips, 2008). Thus, neotropical liana infestation appears to be much more closely tied to forest structure and dynamics than to climatic water availability.

The absence of fragmentation effects on liana infestation in our study was somewhat surprising given expectations based on studies in Amazonian and Atlantic forests (Laurance et al., 2001; Magnago et al., 2017), but suggests again that any effects here were not strong in space or time. After excluding flooded forests, most of our samples were more than 200 m from the nearest edge and were in fragments larger than 800 ha (Table S1), which may have made it difficult here to observe fragmentation and edge effects on liana infestation. Previous research in our study region has indicated that habitat fragmentation does affect forest structure (Reis et al., 2018), and the current study showed that this in turn affects liana infestation (Figure 4). Over time, structural changes induced by drying and increased fragmentation (Reis et al., 2018), as well as the accelerated dynamics of Amazonian forests (e.g. Brienen et al., 2015; Phillips & Gentry, 1994) and impacts of increases in severe drought and in CO_2 concentrations to favour liana growth (Granados & Korner, 2002; Schnitzer & van der Heijden, 2019), may all be contributing to increasing liana infestation in Amazonian forests.

4.1.4 | Forest structure

The structure of each forest, especially the slenderness of its constituent trees, was the most important plot-level feature and the only one to explain significantly the proportion of trees infested by lianas in our plots. The importance of tree slenderness as well as diameter of the trees was confirmed by analyses at the level of individual trees and tree species. While an association between the size of the host tree and liana infestation is consistent with previous findings (Fadrique & Homeier, 2016; Sfair et al., 2013; van der Heijden et al., 2008), whether and how the slenderness of trees predicts liana infestation has been very poorly explored. Our study is the first to reveal its importance in Amazon forests. Larger trees generally are older and, consequently, have had more time to become infested so the liana tree-size association per se is not surprising. But the fact that slenderness (the *H*:*D* ratio) provides an additional explanatory factor, with taller trees for a given diameter being *less* likely to be infested, indicates other processes are at play.

Firstly, liana infestation may itself change the slenderness of the trees, since when we controlled for tree species identity, we found that the most heavily infested individuals from the dominant regional tree species were typically less slender than non-infested trees (Figure S6). A similar pattern has recently been observed in one semi-deciduous seasonal site in the Atlantic forest (Dias, Santos, Santos, & Martins, 2016). Competition with lianas has also been observed to increase allocation to stem thickness at the expense of height for tree saplings in a disturbed forest (Schnitzer, Kuzee, & Bongers, 2005).

Secondly, slender trees may be more susceptible to stem breakage (Ribeiro et al., 2016) and may become more susceptible to breakage-induced mortality when infested by lianas. If so, this would imply that stout trees infested by lianas are more likely to survive liana infestation, rather than simply being more likely to be infested (cf. survivorship bias in Visser et al., 2018). Only an experiment or very long-term observations can fully resolve whether lianas alter tree allometry, potentially as a result of mechanical stress due to liana infestation, or if trees with certain allometric attributes, such as those who are less slender, with the crown more exposed to light may be at higher accumulated risk of liana infestation.

4.1.5 | The impact of identity

Wood density, which is directly linked to diameter growth rate, was an important factor in determining liana infestation at the tree taxon level (Figure 5), with species with the highest wood density and lowest potential growth rate more infested by lianas than fast-growing tree species with low wood densities. Slow-growing tree species have of course had more time to become infested than fast-growing ones (Laurance et al., 2001; Lowe & Walker, 1977; van der Heijden et al., 2008), suggesting that exposure time to liana infestation is an important driver of infestation (Fadrique & Homeier, 2016). For example, in a natural forest in Nigeria, *Sterculia rhinopetala* (Sterculiaceae), trees, which are slow growing had 33% more infestation compared to *Khaya ivorensis* (Meliaceae), which grows much more rapidly (Lowe & Walker, 1977). A similar pattern has also been observed in the Neotropics (Laurance et al., 2001; van der Heijden et al., 2008). Fast growth rate is not the only tree characteristic that can help prevent liana infestation.

Other tree characteristics that have been found to influence the likelihood of liana infestation are monopodial growth

form, flexible stems, large compound leaves and a smooth bark (Clark & Clark, 1990; Putz, 1984b; Sfair, Rochelle, Rezende, & Martins, 2016), which would explain the results here for *S. morototoni* and *J. copaia*, the two species least infested by lianas. The lower infestation rate of faster growing trees has been suggested to result from differential mortality rates, with fast-growing, light-demanding tree species dying quicker than shade-tolerant species when infested by lianas (Clark & Clark, 1990; Visser et al., 2018). If growth-related differential survival rates contribute here to infestation rates, then it suggests that shade-tolerant tree species, which already experience lower light levels than others, are able to survive for long periods with still lower light levels in the crown as a result of liana infestation.

4.2 | Drivers of tree growth

4.2.1 | Liana infestation and light

Lianas strongly affected tree growth rate and the degree of liana infestation was the most important explanatory factor in determining individual tree growth. The negative effect of lianas on tree growth has also been observed in other neotropical forests (Clark & Clark, 1990; Fadrique & Homeier, 2016; Ingwell et al., 2010; van der Heijden & Phillips, 2009; van der Heijden, Powers, & Schnitzer, 2015). The fact that a negative effect of liana infestation on tree growth has now been observed in multiple environments across a large region suggests that this represents a general effect across most tropical forests. The negative impact of lianas on tree growth and tree survival (Ingwell et al., 2010; Phillips et al., 2005) means that lianas significantly impact on the capacity of tropical forests to store and sequester carbon (e.g. Phillips et al., 2002; Tymen et al., 2016; van der Heijden et al., 2015).

We observed not only that heavy liana infestation (>75% COI) affects tree growth but, importantly, that its effects depend also on the light received by the tree crown. By covering the tree crown with their leaves, lianas limit the amount of light received by tree leaves, which will reduce photosynthetic rates (Clark & Clark, 1990; Fauset et al., 2017), and the impacts of this for any given level of liana infestation are much more powerful when lianas infest canopies which are otherwise well-lit. Thus, lianas act to effectively homogenize the light conditions experienced by trees in the forest. They therefore reduce the advantage that taller trees and others growing in high light conditions receive and may equalize the competitive playing field between trees in the tropical forest.

Overall, we showed that the physical structure of forests (tree diameter and slenderness) and species identity are more important than climatic or soil factors in determining liana infestation across the southern border of Amazonia. Despite the large differences in liana infestation between the sites, this was not related to climate or habitat fragmentation, suggesting that increases in liana infestation observed over recent decades are not directly related to these factors, at least in Southern Amazonia. Instead, these variables may indirectly impact the degree of liana infestation by their impact on forest structure (Reis et al., 2018), which is clearly an important determinant of liana infestation. Furthermore, our results indicate variation in liana infestation between individual trees and species that may be explained by variables related to tree allometry, age or growth rate, with larger and less slender trees and slower-growing species, more often infested by lianas. Thus, exposure time is a potentially important driver of liana infestation. We also showed that lianas may reduce the growth rate of the trees, especially for trees growing in well-lit conditions. Thus, in all, liana increases are capable of affecting the structure, stand-level growth, floristic composition and reproductive success of tropical forests and trees (García-León, Martínez Izquierdo, Mello, Powers, & Schnitzer, 2018; van der Heijden et al., 2015). Not only do lianas reduce the capacity of forests to sequester atmospheric carbon dioxide, but they also affect competitive interactions among their tree species, and hence are capable of altering their tree biodiversity.

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AUTHORS' CONTRIBUTIONS

S.M.R. wrote the manuscript with input from all authors (B.S.M., P.S.M., F.E., A.E.-M., B.H.M.Jr., S.F., E.A.d.O., G.M.F.v.d.H., D.G., T.R.F. and O.L.P.); B.S.M. and O.L.P. were involved in planning and supervised the work; S.M.R., B.S.M., B.H.M.Jr., P.S.M., E.A.d.O., F.E. and A.E.-M. performed the field measurements; S.M.R., P.S.M., F.E. and A.E.-M. performed the analyses and made the figures. All authors discussed the results and contributed to the final manuscript.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/1365-2745.13470.

DATA AVAILABILITY STATEMENT

The data are available as a data package on ForestPlots.net: https://doi.org/10.5521/forestplots.net/2020_5 (Reis et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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